Soil wetting decreases the level of apparent activation energy for microbial respiration in subtropical forest ecosystems

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Abstract:

Apparent activation energy (Ea) is one of the most important and sensitive parameters that control soil organic C (SOC) decomposition in prevailing earth system models (ESMs). The variation of apparent Ea is affected by multiple soil environmental factors, among which soil moisture exerts a strong effect. Aiming to better inform temperature sensitivity parameterization in ESMs, here we examined the relationship between apparent Ea and soil moisture with both incubation experiment and field measurement in subtropical forests. We found that apparent Ea declined as soil moisture increased, consistently in both incubation and field experiments. We speculated that this phenomenon was due to altered microbial community composition from changing soil moisture. Our results suggest that future warming and changing precipitation would significantly affect the decomposition of recalcitrant carbon pools in subtropical forests. Lacking representation of the impact of soil moisture on SOC decomposition temperature sensitivity in current ESMs might have biased climate projection.

1. Introduction

Activation energy (Ea), a measure of the minimum energy required to start a chemical reaction, is often synonymously referred to the temperature sensitivity of soil organic carbon (SOC) decomposition based on Arrhenius equation (Davidson *et al.*, 1998; Craine *et al.*, 2010a; Craine & Gelderman, 2011; Sierra, 2012). For example, Craine (2010) tested landscape-level variations in temperature sensitivity (apparent Ea) of labile SOC in a grassland ecosystem. Moreover, the relationship between temperature sensitivity and apparent Ea was discussed via recalcitrant organic matter-Ea relationship for different soils. It has been found that increase in reaction rate (= the Q_{10} value) is larger for reactions with higher Ea. In other words, higher Ea results in less reactive and more recalcitrant SOC (Davidson & Janssens, 2006; Kleber, 2010; Sierra, 2012).

Predicting the temperature sensitivity of microbial decomposition is vital to projecting the responses of soil carbon dynamics to future climatic change and terrestrial ecosystem function (Friedlingstein *et al.*, 2006; Schuur *et al.*, 2009). The backbone of predicting microbial decomposition is the Arrhenius equation, which provides a solid theoretical framework for the temperature sensitivity of a variety of biochemical recalcitrance or substrate (Sierra, 2012). Earth system models (ESMs) (Davidson *et al.*, 2012; Wieder *et al.*, 2015a) equipped with those detailed microbial processes and relied on Arrhenius-type temperature sensitivity parameterization have showed a promising capability to project responses of soil carbon dynamics to climate change (Wieder *et al.*, 2015b). In these models, Ea, which is used to describe the reaction response to temperature under optimal conditions (Wang *et al.*, 2012), has been considered as one of the most important parameters determining SOC decomposition and its underlying processes (Allison *et al.*, 2010; Wieder *et al.*, 2015a).

During the past decade, the relationship between apparent Ea and substrate quality was controversial for non-labile or low-quality organic matter decomposition studies (Luo *et al.*, 2001; Fang *et al.*, 2005; Sierra, 2012). Recent studies focus on the relationship between Ea

and abiotic and biotic drivers such as microbial respiration, topographic position, landscape-level variation, and pH for different soils (Craine *et al.*, 2010b; Wang *et al.*, 2012). In spite of investigation for the impacts of environmental variables on apparent Ea, few studies have examined the effect of soil moisture on the apparent Ea of microbial respiration (Davidson & Janssens, 2006; Kleber, 2010; Zhou *et al.*, 2011; Suseela *et al.*, 2012a; Ding *et al.*, 2016; Hursh *et al.*, 2016). Moreover, Ea-soil moisture relationship has not yet been coupled into large-scale models (Wieder *et al.*, 2015a), because their relationship is not still clearly understood at microbial process levels. Thus, an improved understanding of Ea-moisture relationship is required to inform better representation of SOC decomposition in those ESMs.

Subtropical ecosystems process more carbon annually than other regions of the Earth (Holland *et al.*, 2000). Therefore, understanding Ea-moisture relationship is needed to better quantify responses of soil carbon pool to climatic change in this region, as illustrated by the carbon-quality temperature (CQT) hypothesis. Besides, the subtropical forests (e.g. southern China) experience more significantly changes in precipitation regimes compared to other tropical forests (Tang et al., 2006) due to its unique climate regime. Moreover, both long-term observation data and model simulations have suggested a significance decreasing trend in soil moisture of subtropical forests (Zhou *et al.*, 2011) due to changing precipitation pattern (Liu *et al.*, 2016; Luo *et al.*, 2017). Thus, the variation in moisture among forest soils provides a golden opportunity for studies of the relationships between apparent Ea and soil moisture under different moisture conditions. Although many studies indicated that the declining soil moisture in subtropical forests has constrained root, soil microbial biomass, soil respiration, temperature and moisture sensitivity (Jiang *et al.*, 2013; Xu *et al.*, 2014; Wei *et al.*, 2015), the effect of decreasing trend on apparent Ea has still not been investigated. The lack of examination could be due to limited precipitation manipulation experiments (Beier *et al.*, 2012), or be ascribed to the complexity of apparent Ea-moisture relationship among different soils or different topographic positions (Craine *et al.*, 2010b).

This work is motivated by the needs to enhance the understanding of Ea-moisture relationship, so to improve projection of responses of SOC to environmental changes. Here

we hypothesize that apparent Ea would decrease with increasing soil moisture, as high soil water content could reduce temperature sensitivity (Davidson *et al.*, 1998; Suseela *et al.*, 2012b). As intrinsic Ea-moisture relationship has not yet been investigated in laboratory experiments or field soils alone (Wang *et al.*, 2012), to test our hypothesis, we used a combination of both laboratory incubation experiments and field measurements.

2. Material and methods

2.1 Site description

The experiments were conducted in four subtropical forests in Guangdong province, southern China. The BF (climax evergreen broadleaved forest, more than 400 years old, coverage 95%) and CF (mixed coniferous and broadleaf forest, about 110 years old, coverage 90%) sites are located at the Dinghushan Biosphere Reserve (DBR:112° 30'~112°33′E, 23°9′~23°11′N), and the CP (conifer plantation, 26 years old, coverage 70%) and BP (native broadleaved species plantation, 26 years old, coverage 90%; see detail in Wei's paper (2015)) are located at Heshan National Field Research Station of Forest Ecosystems (HSF:112°54′E, 22°41′N), Guangzhou Province, China. Mean annual air temperature is 22.3℃ at the DBR and 21.7℃ at the HSF. Mean annual precipitation is 1678 mm at the DBR and 1700 mm at the HSF. The soils are classified as oxisols in the USDA soil taxonomy, with a bulk density of 1.4g cm^{-3} (table 1).

Tabel 1. Soil characteristics including forest type (evergreen broadleaved forest (BF), coniferous broadleaved mixed forest (CF), coniferous species plantation (CP), broadleaved native species plantation (BP)), total organic carbon (TOC), total nitrogen (TN), total phosphorous (TP), water holding capacity (WHC).

Forest type	WHC (g g^{-1})	TOC (mg g^{-1})	TN (mg g^{-1})	TP (mg g^{-1})	pH
BF	0.31±0.002[d]	25.07±0.73[a]	1.86±0.05[a]	0.22±0.004[b]	3.10±0.02[c]

CF	0.57±0.008[b]	16.95±0.46[b]	1.22±0.02[b]	0.25±0.004[a]	3.32±0.01[b]
CP	0.55±0.004[c]	14.80±0.26[c]	1.05±0.01[c]	0.19±0.008[c]	3.58±0.08[a]
BP	0.59±0.004[a]	13.30±0.32[d]	0.99±0.02[c]	0.22±0.05[b]	3.34±0.02[b]

mean±standard error, superscripts denote significant differences in WHC, TOC, TN, TP and pH among forest types (p<0.05).

2.2 Experimental Design

For field measurement, three 10×10 m^2 quadrats were firstly established in each forest. Each quadrat contained three 1×1 m^2 plots, which were trenched for measuring heterotrophic respiration (R_h). Trenching and collar installations were performed in November 2009. We measured soil R_h using a portable CO_2 analyzer (Li-8100 Auto Soil CO_2 Flux system, Li-Cor Bioscience, NE, US) with a frequency of twice per month (normally on rainless days at the beginning and in the middle of a month) from February 2010 to January 2012. At the same time, soil temperature and moisture at 5cm depth were also recorded. One soil core was collected from the surface soil (0 - 20 cm) using a circular soil collector with 4-cm inner diameter in each plot each month (normally after the second CO_2 measurement each month) and the three soil cores in the same quadrat were mixed as a composite sample. We therefore had three composite soil samples in each of the four forests per month during the investigation period (see Wei *et al*., 2015 for full details).

For incubation experiment, four random surface soil cores (0-20cm), each of which were re-collected and mixed by five soil cores, were chosen at each forest. After collection, soils were passed through 2-mm sieve with apparent plant roots and stones being removed (Zhou *et al.*, 2014). For each sample, we measured total organic C and total N concentration, water holding capacity (WHC) (Bailey et al., 1991), and pH in a 1:1 mixture of soil and water. After

sieving, all soils had their soil moisture adjusted to either 20%, 40%, 60%, 80% water holding capacity (WHC). Four replicates of each forest were then incubated at five different temperatures (10℃, 17℃, 24℃, 31℃, 38℃) with an additional 6 replicates incubated at the same temperature. Three flasks (or replicates) of each treatment were harvested on days 7 and 90 in order to measure microbial biomass carbon (MBC), dissolved organic carbon (DOC), total organic carbon (TOC), total nitrogen (TN), inorganic N (NH_4^+ and NO_3^-). Part of the soil at BP forest site in each flask was collected and stored at -20℃ or later analysis of PLFAs of fungal (F) and bacteria (B) on days 7 and 90. Microbial community PLFAs were analyzed according to Bossio and Scow (1998). The details for measuring methods can be found in Zhou *et al* (2014).

2.3 Statistical analysis

We used the Arrhenius equation to calculate the apparent activation energy (Ea), where the rate of soil R_h is described by:

$$R_h = A \quad (1)$$

where T is temperature in Kelvin, R is the gas constant (8.314 J K^{-1} mol^{-1}) and A is the frequency factor that is specific to each reaction and generated independently for each set of four replicates. Specifically, apparent Ea was calculated as the slope of the relationship between -1/RT and the natural logarithm of respiration rates.

Significance differences between treatments were determined with Tukey's HSD post-hoc tests. One-way ANOVA and Pearson correlation were used to analyze soil moisture, soil microbial and chemical properties effect on apparent Ea. The relationship between apparent Ea and soil R_h from field data was fitted with nonlinear least square method. All analyses were conducted in Matlab (R2014a).

3. Results

3.1 Soil respiration varied under different treatments

Across all temperature treatments, the average soil R_h of each forest (n=24), which reached the highest during 10 incubation days, declined with incubation days and the average soil R_h at 60%WHC and 80%WHC is higher than that at 20% WHC and 40% WHC (figure 1-4), and the average soil R_h at 20% WHC is the lowest with each forest. In addition, soil R_h responded to moisture levels on days 7, 30 and 90 that represented the early, middle and late incubation stages were analyzed. We found that moisture had a significant effect on soil R_h at all incubation stages at 31℃ and 38℃ of each forest (p<0.05). However, there were only significant differences between moisture and soil R_h at late incubation stage at 10℃, 17℃ and 24℃ of each forest (p<0.05).

3.2 The relationship between apparent Ea and soil moisture from incubation experiments

The average adjusted coefficient of determination (R^2) between temperature and average soil R_h of each forest was 0.84±0.09 across all moisture levels and all time points, by using the Arrhenius equation (n=60, p<0.001). Apparent Ea varied significantly with incubation days across all moisture levels of each forest (table 2, figure 5). Apparent Ea varied from 131.36 kJ mol^{-1} at 40% WHC (BF) to 14.88 kJ mol^{-1} at 80% WHC (CP). The one-way ANOVA analysis showed that apparent Ea of each forest on day 7, 30 and 90 was significantly influenced by soil moisture (p<0.05). To better elucidate the relationships between apparent Ea and soil moisture, we examined relationships between log-transformed apparent Ea and soil moisture
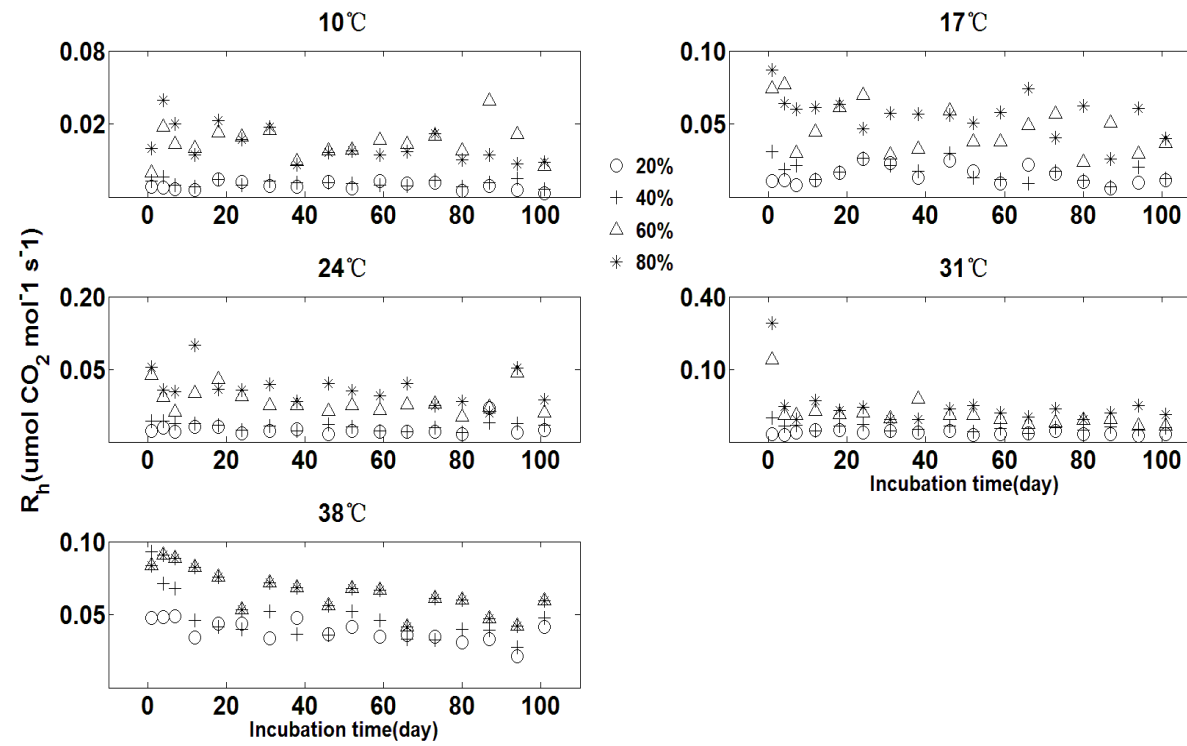
10℃

17℃

○ 20%
+ 40%
△ 60%
* 80%

24℃

31℃

R_h(umol CO_2 mol⁻1 s⁻1)

38℃

Incubation time(day)

Incubation time(day)

Figure
of BF forest
time at different
levels.

1. Changes of R_h
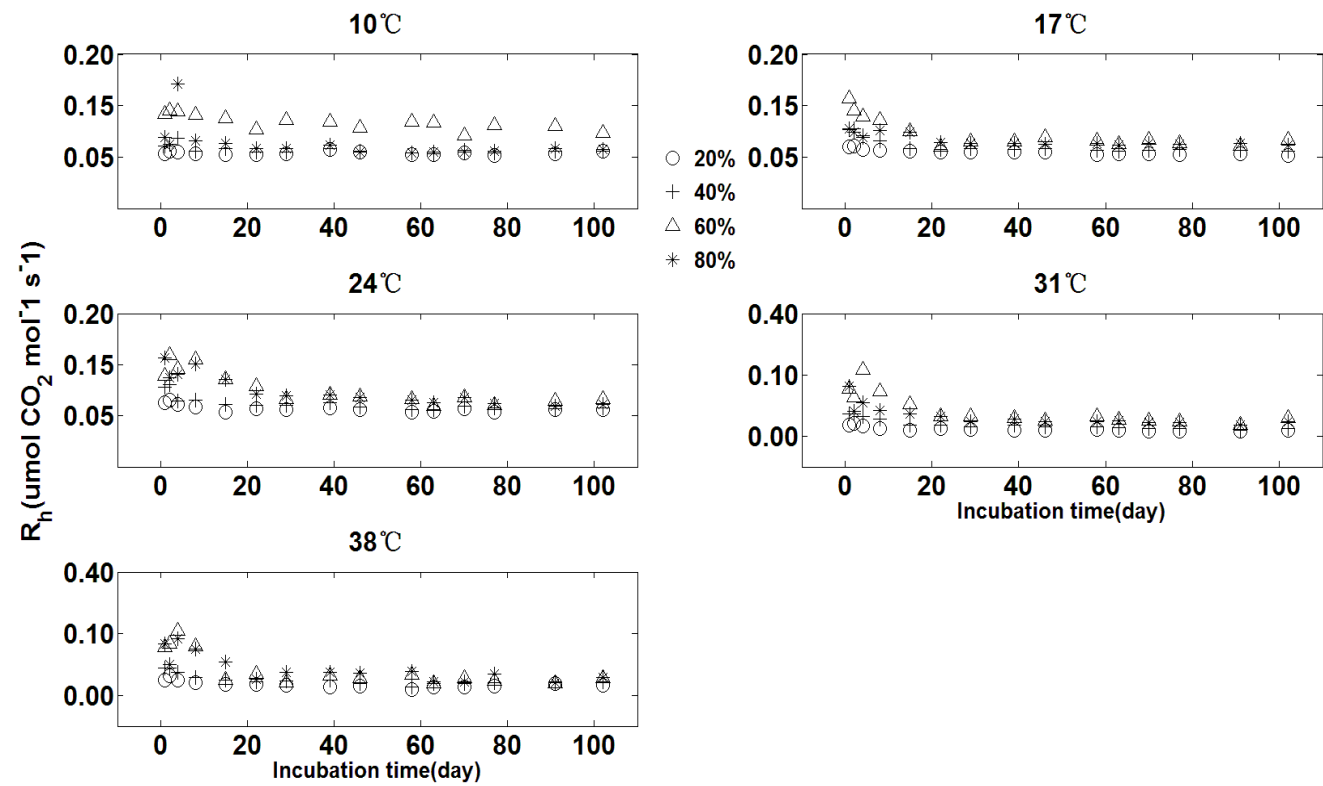with incubation
soil moisture

Figure 2. Rh of with time at different soil moisture levels.
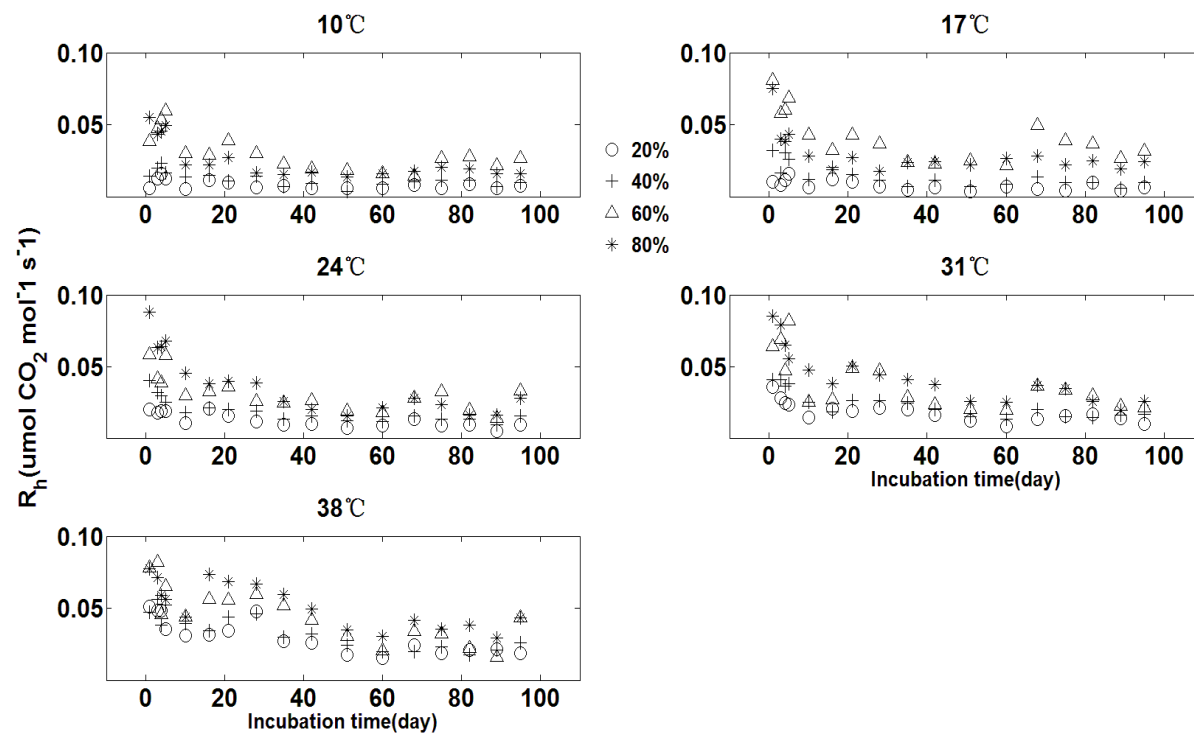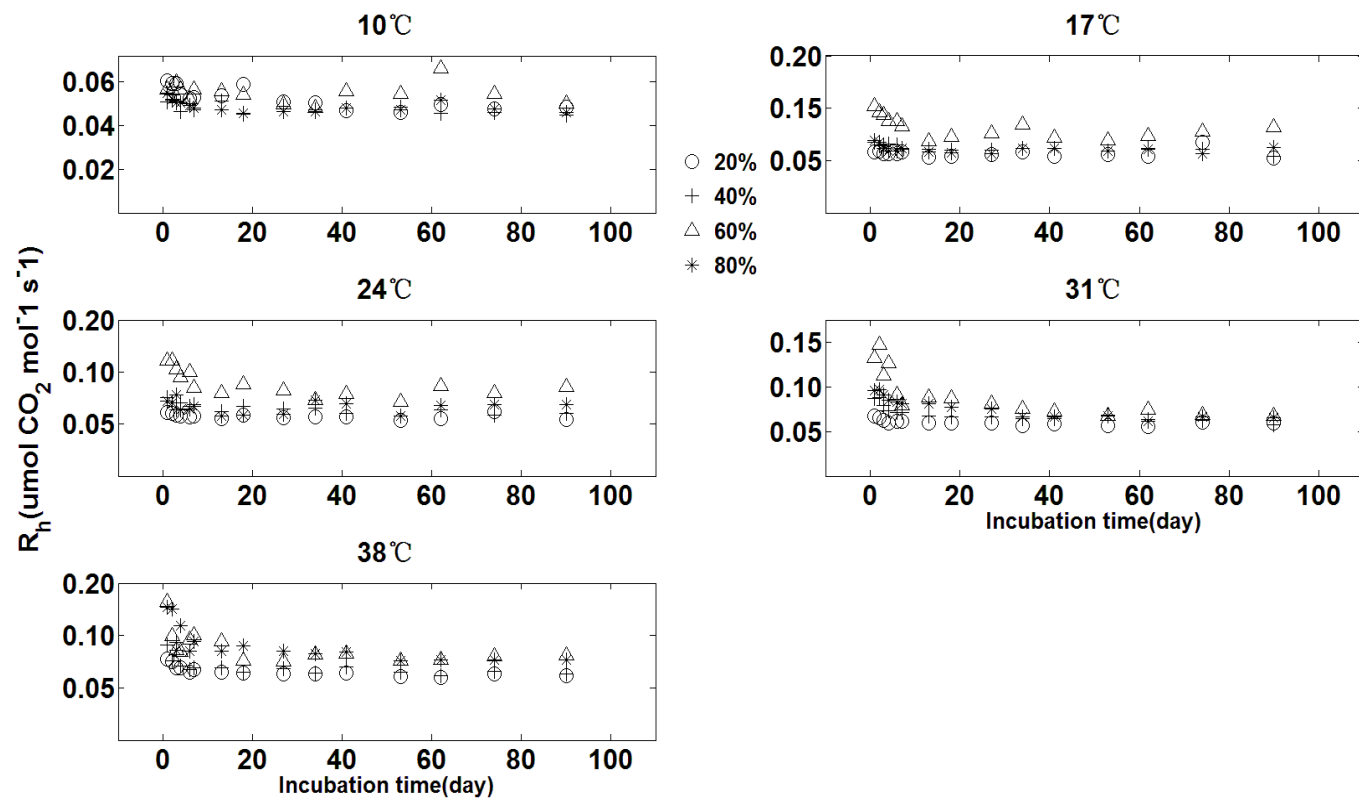
Changes of CF forest incubation

Figure 3. CP forest time at moisture

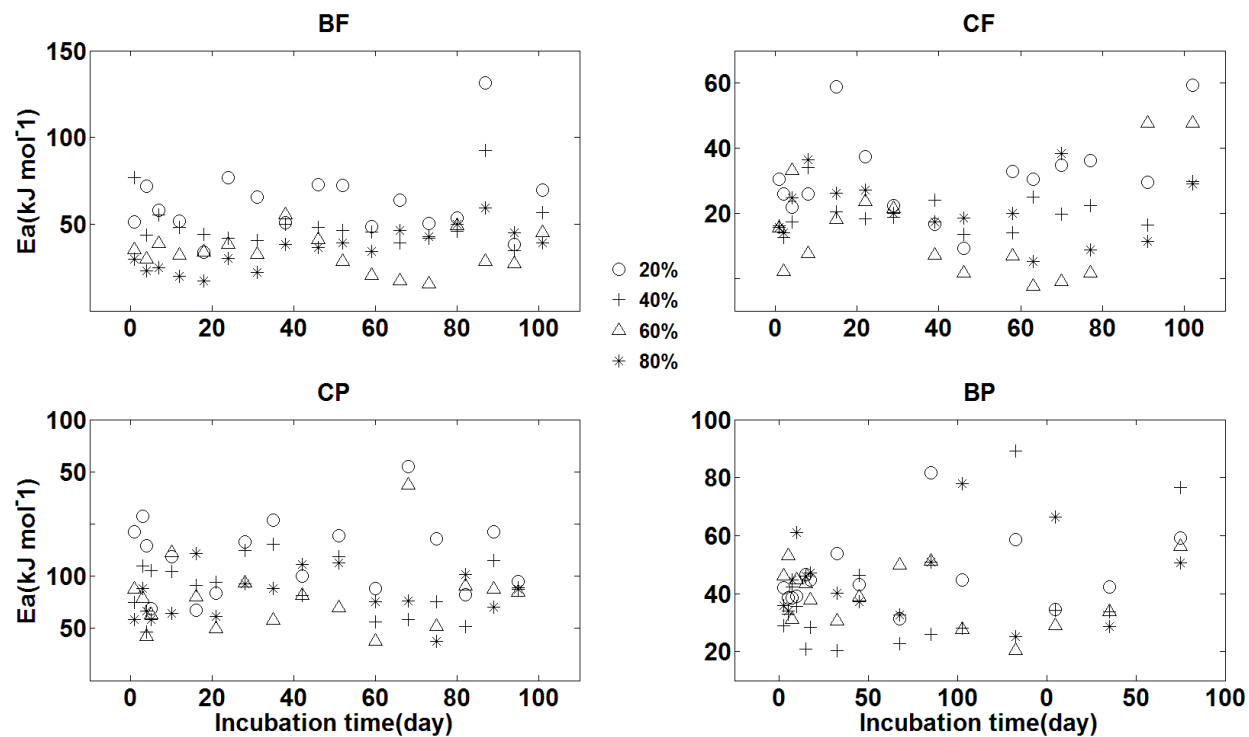Changes of Rh of with incubation different soil levels.

Figure 4. Changes of R_h of BP forest with incubation time at different soil moisture levels.

Figure 5. apparent forest time at moisture

Changes of Ea of each with incubation different soil levels.

after standardizing differences in average apparent Ea of each forest. The average apparent Ea **of individual forest decreased linearly with increasing soil moisture (r=-0.85, p<0.001; figure** 6), with 24 kJ mol^{-1} greater Ea at 20% WHC (58.6 kJ mol^{-1}, BF) than at 80% WHC (34.9 kJ mol^{-1}, BP).

Table 2. Average apparent Ea of each forest with different moisture levels

	20%	40%	60%	80%
BF	62.38[a]	50.08[a]	33.33[b]	35.23[b]
CF	51.44[a]	40.18[ab]	35.34[b]	40.82[ab]
CP	48.06[a]	35.93[b]	32.06[b]	32.28[b]
BP	46.56[a]	37.69[b]	39.47[b]	45.21[b]

Superscripts denote significant differences in apparent Ea of each forest with moisture levels.

3.3 The relationship between apparent Ea and soil properties

A positively significant influence of moisture treatments on MBC/DOC ratios (p<0.01) and negative effects on the PLFA concentrations of F:B ratio (figure 7) at BP forest site on day 7 and 90 (p<0.01) (decreasing fungi and increasing bacteria) were detected with the same incubation temperature. The relationship between apparent Ea and MBC/DOC ratio was analyzed on day 7 and 90 at four forest sites. However, no significant Pearson correlation was found between apparent Ea and MBC/DOC with different soil moisture levels under the same incubation temperature. Meanwhile, the relationship between apparent Ea and F:B ratio also was analyzed at BP forest site on day 7 and 90. A significant correlation between apparent Ea and F:B ratio was only detected on day 7 (average r=0.62) and 90 (average r=0.83) with the same incubation temperature. For other properties (inorganic nitrogen and TN), we did not find a significant correlation with Ea (p>0.01).
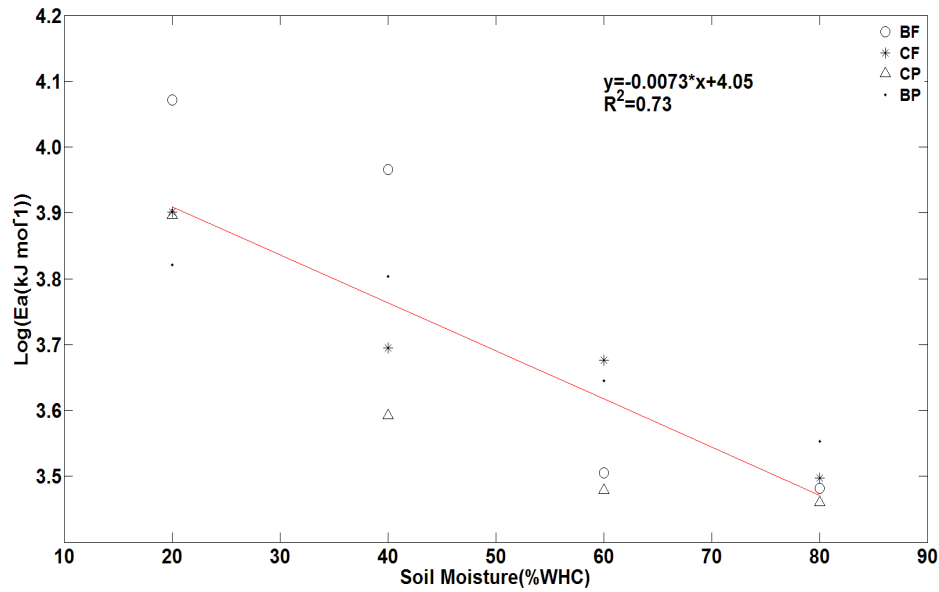
Figure 6. Relationship between apparent Ea of each forest and soil moisture from incubation experiments.
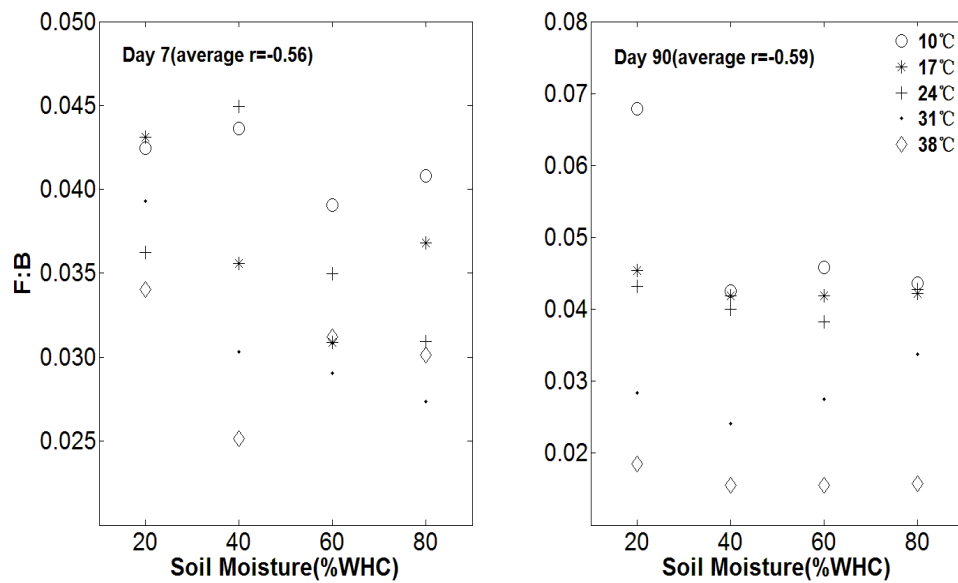

Figure 7. Relationship between F:B ratio and soil moisture in BP forest on day 7 and 90.

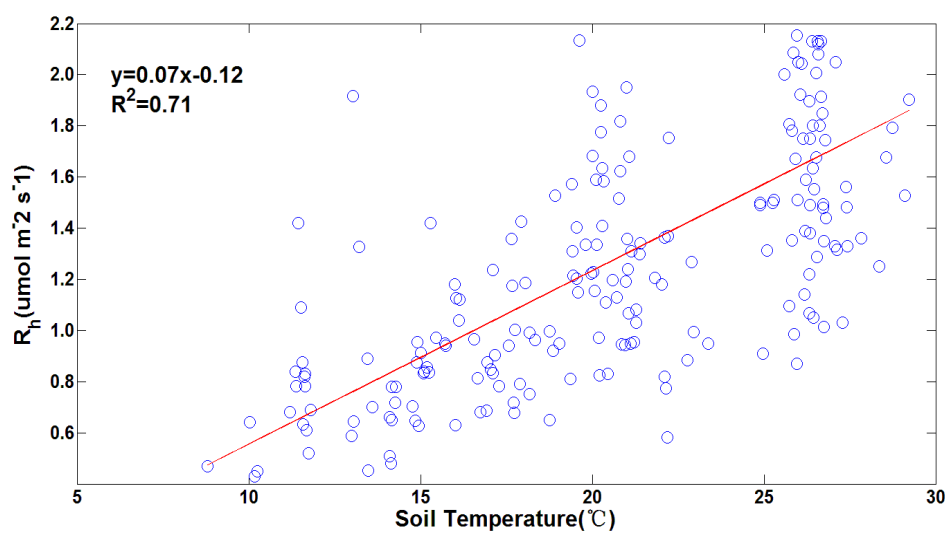*3.4 The relationship between apparent Ea and soil moisture from field measurements*

The soil R_h, which increased with soil temperature, followed Arrhenius equation at 5cm depth (adjusted R^2=0.5, n=216, p<0.001; figure 8a). In order to investigate the apparent Ea-soil moisture relationship from field data, four soil moistures levels (each soil moisture level

included 40 pairs of data) were firstly identified and then corresponding apparent Ea was matched. The results indicated that soil moisture had a significance impact on Ea. Ea of lower soil moisture (0.12%-0.28%) was lower significantly than that of higher soil moisture (0.33%-0.38%) (figure 8b). According to Crain (2010), there is a linearly decreasing correlation between log-transformed apparent Ea and log-transformed relative respiration rates at 20℃ (R_{20}) ($\log(Ea) = 2.01-0.094*\log(R_{20})$). To test the relationship between apparent Ea and soil moisture, we pooled R_{20} from field data together from four forests sites (average soil temperature is 20.27, n is 12) (figure 9). As seen in figure 9, the apparent log-transformed Ea significantly declined with increasing soil moisture (r=-0.71, p<0.001).

4. Discussion

Our results suggest that soil R_h is affected by soil moisture. Regardless of temperature treatments, soil R_h at lower moisture levels (20%) tended to be lower than that of other moisture levels, which has been attributed to soluble substrate limitation, thereby resulting in low microbial activity (Reichstein *et al*., 1983). However, soil R_h at higher moisture level is mainly limited by oxygen (Orchard and Cook, 1983). Soil R_h at 60% WHC that is the optimal moisture level tends to be higher, because higher microbial activity might override the influence of oxygen limitation (William. 2007). We also found that the effect of moisture levels on soil R_h at different stages varied with temperature treatments. These results indicate that the responses of soil R_h to moisture levels are controlled by incubation temperature and
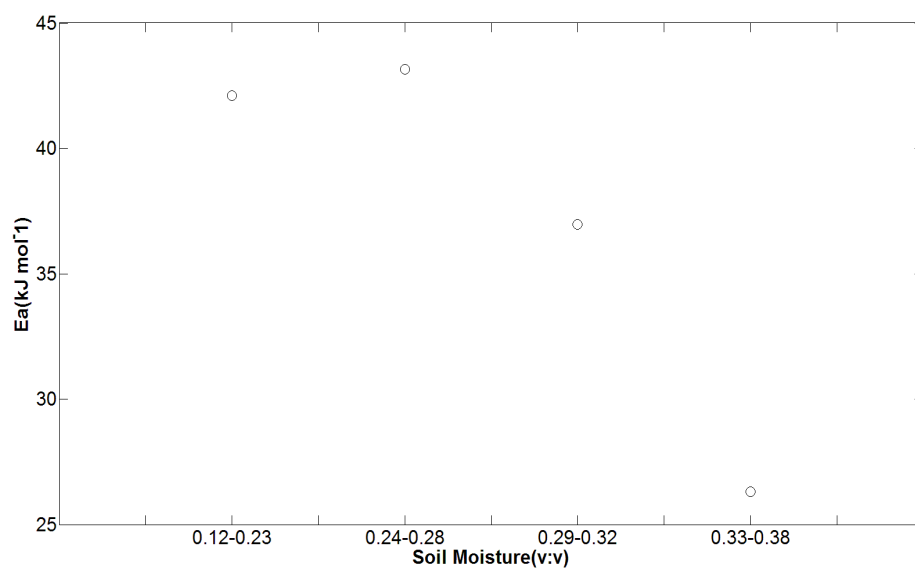
a)

Figure 8. a) Relationship between R_h and soil temperature from field measurements; b) Relationship between apparent Ea and soil moisture from field measurements.
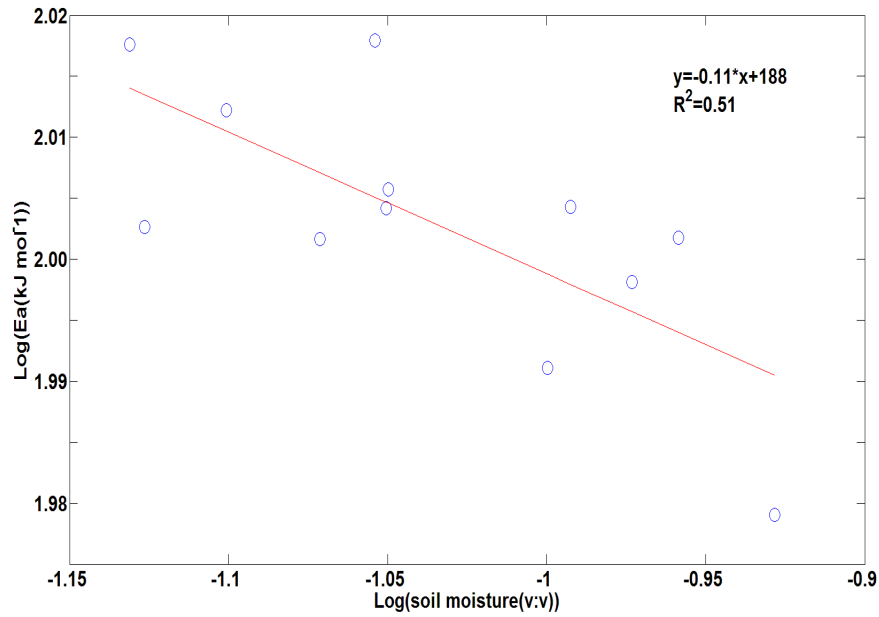
limitation of soluble substrate and oxygen concentration.

Figure 9. Relationship between apparent Ea and soil moisture at soil temperature 20℃ with

field measurements.

Our results show that the apparent Ea decreases with increasing soil moisture.

Considering the relation of apparent Ea, Q_{10} and F:B ratio, the relationship between apparent

Ea and soil moisture could be explained by their connections with oxygen concentration and

microbial communities. First, higher soil moisture could reduce the diffusion of oxygen over

a substrate during aerobic respiration (Davidson *et al.*, 2012), impede microbial production of

CO_2, thereby reduce temperature sensitivity (Q_{10}) of reaction rates (Davidson *et al*., 1998).

Therefore, apparent Ea also decreases because Q_{10} and apparent Ea are positively linked with

each other (Kleber, 2010). On the other hand, the relationship between apparent Ea and soil

F:B ratio also shows that apparent Ea is affected by soil microbial communities. Because

bacterial communities increase with increasing soil moisture, leading to more decomposition

of labile substrate (lower apparent Ea), thereby resulting in decrease in apparent Ea. In our

study, no significant correlation between apparent Ea and MBC/DOC ratio deserves

discussion. Although substrate concentration such as MBC or DOC also controls enzyme

respiration reaction in Michaelis-Menton kinetics, no significant correlation is found between

apparent Ea and MBC/DOC ratio with different soil moisture levels that had a significance impact on MBC/DOC ratio. High soil water might increase substrate availability, however, microbial substrate decomposition can be strongly limited due to alteration of microbial communities or cell energy demands (Schimel & Weintraub, 2003) even if substrate availability is unlimited. This means that soil water changes substrate availability by altering the composition and activity of decomposer microbes (Williams, 2007). In all, apparent Ea-moisture relationship is collectively controlled by soil oxygen concentration and microbial communities.

Apparent Ea is closely linked to recalcitrant substrates, which means that the more recalcitrant carbon pool, the more apparent Ea, according to CQT hypothesis (Fierer *et al.*, 2003). The increasing apparent Ea implies that more recalcitrant carbon would be decomposed with the decline in soil moisture. In the future, more soil CO_2 emission and a stronger carbon-climate feedback would be triggered due to the increase in temperature sensitivity (apparent Ea) of subtropical SOC as a result of climate warming and soil moisture decline. This contradicts a previous study that claimed that soil respiration would decrease in subtropical forests if soil moisture continues to decrease (Jiang *et al.*, 2013).

To date, apparent Ea-moisture relationship has not yet been incorporated into ESMs. Recently, 3 out of 4 published microbial models have incorporated the soil moisture effect on soil enzymatic processes (Wieder *et al.*, 2015a) based on DAMM module that considers soil moisture impact on substrate and oxygen supply (Davidson *et al.*, 2012; Zhang *et al.*, 2014). In these models, apparent Ea is a sensitivity parameter with a fixed value that intrinsically represents temperature sensitivity of enzymatic-processes (Davidson *et al*., 2012). However, our study demonstrated a linear relationship between apparent Ea and soil moisture. These observed apparent Ea-moisture relationships could be considered in ESMs to capture the response of SOC to future warming and precipitation pattern changes.

There are inherent uncertainties in our findings from three aspects. First, the effect of incubation time on Ea has not been accounted for in this study. Second, only oxisol soils were tested at different forest sites, which might have led to potential biases in the findings as

Craine *et al* (2012) showed the relationship between Ea_{20} and R_{20} differed across 28 sites. Third, while we used WHC as a metric of soil water content, matric potential is a more appropriate expression than either volumetric or gravimetric water content. This is because when soil water content is sufficiently low, the expression of matric potential of water available to the organisms is applicable to all soil textures (Davidson *et al.*, 1998; Suseela *et al.*, 2012b). The connection of water matric potential and apparent Ea will be discussed in our next study.

5. Conclusions

Because explicit Ea-moisture relationship has not yet been examined in laboratory experiments or field soils, this study fills the knowledge gap with both field measurements and incubation experiments. Our study showed that apparent Ea decreased with the increasing soil water content in both incubation experiment and field settings. Soil microbial communities and oxygen concentrations were the dominant factors controlling the apparent Ea-moisture relationship. We expect that incorporating this observed relationship into microbial process-based models could improve the prediction of soil microbial respiration. Further studies combining incubation experiments and field observations remain needed to explore how soil moisture affects apparent Ea across different climate regimes, topography, soils and land cover types.

Authorship

WS designed the study; WZ and HW conducted the laboratory incubation and field

measurement; GH, WZ, HW analyzed the data; GH wrote the paper, and all authors edited drafts and contributed to the revisions. The authors declare no competing financial interests. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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